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叶芽花芽需热量差异导致植物先花后叶*

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摘要: 为探究植物先花后叶的影响因素, 本研究以 1963-1988 年间北京地区杏和山桃展叶和始花物候资料及相应的日最高、最低温度数据为基础, 利用偏最小二乘回归法确定杏和山桃叶芽及花芽的需冷期和需热期, 进而利用动态模型和生长度小时模型分别估算叶芽和花芽的需冷和需热量。结果表明, 依据长期物候观测资料, 利用偏最小二乘回归法进行植物需冷和需热量的估算非常有效。先花后叶植物叶芽和花芽需冷量几乎相同, 需热量的差异是导致植物先花后叶的主要原因。杏和山桃花芽的需热量分别为 2 829. 7±876. 2 和 1 457. 2±581. 2 生长度小时, 而相应叶芽需热量却是花芽的两倍之多。基于物候观测的重要性及实用性, 中国物种水平上的地面观测应得到进一步深入发展。

关键词: 先花后叶植物; 需冷量; 需热量; 叶芽; 花芽
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Differences in Heat Requirements of Flower and Leaf Buds Make Hysteranthous Trees Bloom before Leaf Unfolding

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Abstract: To clarify which agroclimatic requirements control the sequential occurrence of flowering and leaf unfolding in hysteranthous plants, Partial Least Squares (PLS) regression analysis was used to identify the chilling and forcing period of leaf and flower buds. The Dynamic Model and the Growing Degree Hour Model were applied to estimate the chilling and heat requirement for leaf unfolding and flowering, based on the phenological records of apricot and mountain peach and daily maximum and minimum temperature data in Beijing during 1963-1988. The results indicated that PLS regression analysis is a useful approach to calculate the chilling and heat requirements of plants when long term phenological observations are available. Leaf and flower buds were found to have similar chilling requirements but different heat requirements, which explained the earlier occurrence of flowering compared to leaf unfolding. The heat requirements of flower buds of apricot and mountain peach were 2 829. 7±876. 2 and 1 457. 2±581. 2 Growing Degree Hours, respectively, while heat requirements of vegetative buds were almost twice as high. In view of the importance and usefulness of phenological observations, species-level ground observations in China should be continued and extended.

Key words: Hysteranthous plant; Chilling requirement; Heat requirement; Leaf bud; Flower bud

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In nature, plants have different strategies to determine the chronological sequence of leafing and flowering. Most woody plants unfold leaves first, before initiating bloom. However, some trees display hysteranthous behavior, meaning that bloom early in spring, before leaves have developed. Earlier flowering than leaf unfolding hold important ecological significance on pollination since abundant flowers sprouting together is prone to attract more insects and no leaf covering facilitates wind pollination meanwhile. Most hysteranthous plants belong to the Rosaceae, Calycanthaceae, Magnoliaceae and Oleaceae families (Kang and Jin, 2009). Even though many hysteranthous trees are widely used as ornamentals or for fruit production, few studies have investigated the causes of this behavior.

Most woody plants from temperate and cool subtropical climates fall dormant in winter to resist unfavorable conditions and to protect the sensitive leaf and flower buds from frost (Luedeling *et al.*, 2013; Jones *et al.*, 2013). It is commonly assumed that dormancy is composed of an endodormancy phase, followed by an ecodormancy period (Lang *et al.*, 1987). The fulfillments of the chilling and heat requirements of plant buds help to break endodormancy and ecodormancy (Campoy *et al.*, 2011; Luedeling, 2012). After breaking dormancy, buds can sprout and develop into leaves and flowers. Numerous studies have been conducted to estimate the chilling requirement of flower buds, since insufficient chilling can cause uneven and even failed bloom, potentially threatening the production of some horticultural crops (Lang *et al.*, 1987). Comparative studies of the chilling and heat requirements of leaf and flower buds are rare. Gao *et al.* (2001) compared the chilling requirements of leaf and flower buds for some hysteranthous fruit trees, and found that flower buds need equal or slightly more chilling units than leaf buds, indicating that different heat requirements of leaf and flower buds might dominate the sequential occurrence of flowering and leafing.

The objectives of the present study were to compare the chilling and heat requirements of leaf and flower buds of two hysteranthous plants, and to identify the agroclimatic triggers that are responsible for earlier occurrence of flowers compared to leaves. In this analysis, we used a chilling and a forcing model to calculate daily chilling and heat accumulations during 1963–1988 in Beijing based on daily maximum and minimum temperatures. A novel method (Partial Least Squares regression) was applied to identify the chilling and forcing periods by relating the leaf unfolding and flowering dates of two hysteranthous trees to daily chilling and heat accumulations. Based on regression results, chilling and heat requirements of both leaf and flower buds of apricot and mountain peach were estimated and compared.

1 Materials and methods

1.1 Phenological and climatic data

There is a long history of phenological observations in China. The Chinese Phenological Observation Network (CPON), which was established in the early 1960s, conducted standardized, systematic and comprehensive phenological observations of plants and animals across China, but unfortunately, was interrupted after 1988 (Lu *et al.*, 2006). Since then, no detailed and nationwide observations have been conducted. Consequently, CPON records before 1988 are highly valuable resources for phenology research in China.

In our analysis, two hysteranthous plants (apricot and mountain peach) in Beijing Summer Palace (40°01′N, 116°20′E, 50 m a.s.l.) were chosen for analysis since these two trees had the longest phenological records there. First leaf unfolding and flowering dates of apricot (*Prunus armeniaca* L.) and mountain peach (*Prunus davidina* Franch.) during 1963–1988 were acquired from the CPON. Details of the phenological observation method have been described by Lu *et al.* (2006).

Daily minimum and maximum temperatures in Beijing during 1963–1988 were obtained from the Beijing Meteorological Station which is only 2.5 km

from the Summer Palace, so that temperatures recorded there should closely mirror conditions at the observation site. Since most common chilling and forcing models require hourly temperature data, idealized daily temperature curves with an hourly resolution were constructed based on daily minimum and maximum temperatures as suggested by Linvill (1989, 1990). Other inputs for the calculation also included sunrise and sunset time, as well as day length, and computed according to the methods used by Spencer (1971) and Almorox *et al.* (2005).

1.2 Chilling/forcing periods and chill/heat requirements for leafing and flowering

Based on the hourly temperature data, the Dynamic Model was used to calculate daily chilling accumulations during 1963–1988. This model was chosen, because it has repeatedly been shown to be the most robust and accurate among commonly used chilling models (Ruiz *et al.*, 2007; Campoy *et al.*, 2011; Zhang and Taylor, 2011; Luedeling and Gassner, 2012). The Growing Degree Hour Model (GDH) was used to calculate daily heat accumulations. The mathematical functions of the chilling and forcing models were given in Luedeling *et al.* (2009a, b). Daily chilling and heat values were subjected to a 15-day running mean to ensure the emergence of recognizable response patterns in subsequent statistical analyses (Luedeling *et al.*, 2013; Luedeling and Gassner, 2012).

Partial Least Squares (PLS) regression was used to identify the chilling and forcing periods for leafing and flowering by relating leaf-unfolding and flowering dates of trees to daily chilling and heat accumulations during 1963–1988, respectively. The PLS regression has proven to be a useful and reliable method when independent variables are highly autocorrelated and when the number of independent variables exceeds the number of dependent variables (Yu *et al.*, 2010, 2012; Luedeling *et al.*, 2013; Luedeling and Gassner, 2012). The two major outputs of PLS analysis are the variable importance in the projection (VIP) and standardized model coefficients. The VIP values reflect the importance of all independent variables for explaining variation in the dependent variables. A threshold value of 0.8 is typically used for determining importance. The standardized model coefficients indicate the strength and direction of the effects (Luedeling *et al.*, 2013).

In the output of PLS regression analysis, VIP values greater than 0.8 and negative model coefficients indicate that positive deviations of the respective independent variable are correlated with early occurrence of bloom or leaf unfolding. In other words, the method identifies periods during which high accumulation rates of chill or heat are related to early occurrence of phenological stages. According to common understanding of the progression of trees through the dormancy period, this should occur during the chilling and forcing periods, respectively. Accordingly, a period when VIP scores for daily chill accumulation rates are predominantly high and model coefficients negative can be considered as the chilling phase. During the forcing phase, the same pattern should emerge for daily heat accumulation rates.

We identified chilling and forcing periods for generative and vegetative buds of apricot and mountain peach and calculated chilling and heat requirements as the total chilling and heat units accumulated during these phases.

All analyses were conducted in the R 2.15.2 programming language. All procedures used in this study were contained in the R package 'chillR' (Luedeling *et al.*, 2013), available at http://cran.r-project.org/web/packages/chillR/.

2 Results

2.1 Chilling and forcing periods for leafing and flowering of apricot

During 1963–1988, the average first leafing and flowering dates of apricot in Beijing Summer Palace were the 18th and 7th of April, respectively, with flowers appearing on average 11 day before leaves unfolded. Daily chilling and heat accumulation rates between the previous May and April were

used as independent variables in the PLS regression, while dependent variables were apricot leaf unfolding and flowering dates, respectively. Based on the VIP and standardized model coefficients of the PLS regression, chilling and forcing periods for leafing and flowering of apricot were identified (Fig. 1-2).

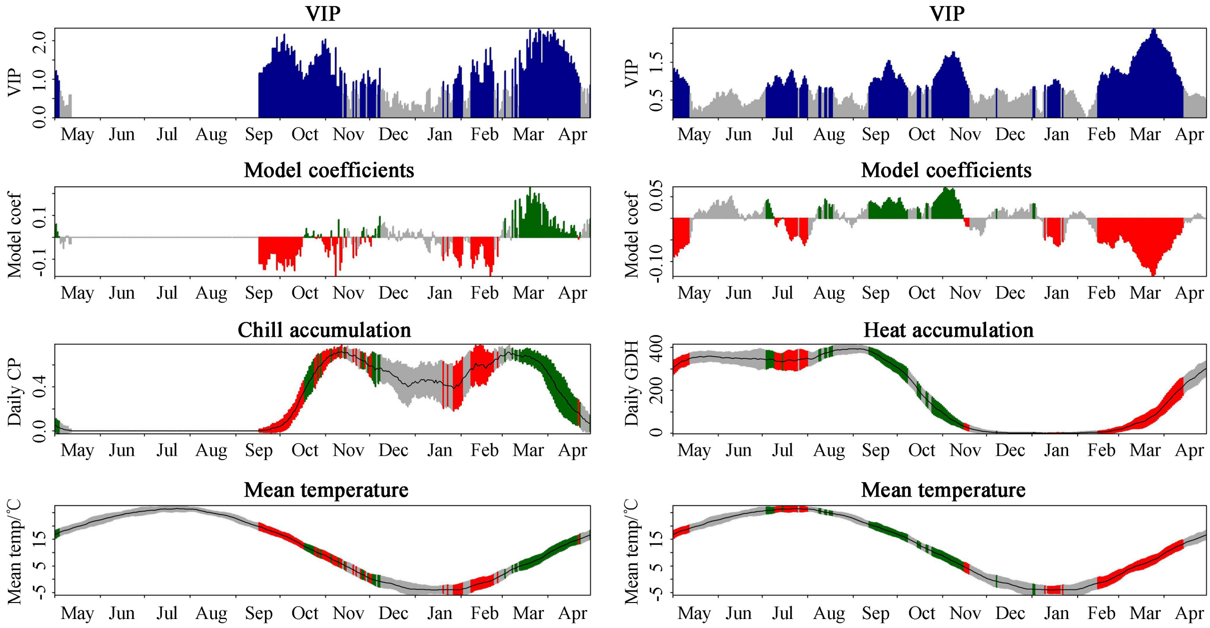

Fig. 1 Results of the PLS regression analysis for flowering of apricot in Beijing, China during 1963-1988. Blue bars in the top row mean that VIP is above 0.8, the threshold for variable importance; while the grey bars mean the VIP is below 0.8. In the second row, red colors mean the model coefficients are negative and important (VIP>0.8), while the green colors indicate positive and important relationships between flowering and daily chilling and heat accumulations. In the third and bottom rows, the grey, red and green bars indicate the standard deviation of daily chilling and heat accumulation and mean temperature. The left part of the figure is the PLS analysis result for the chilling period, while the right part is for the forcing period. CP means Chill Portions and GDH means Growing Degree Hours

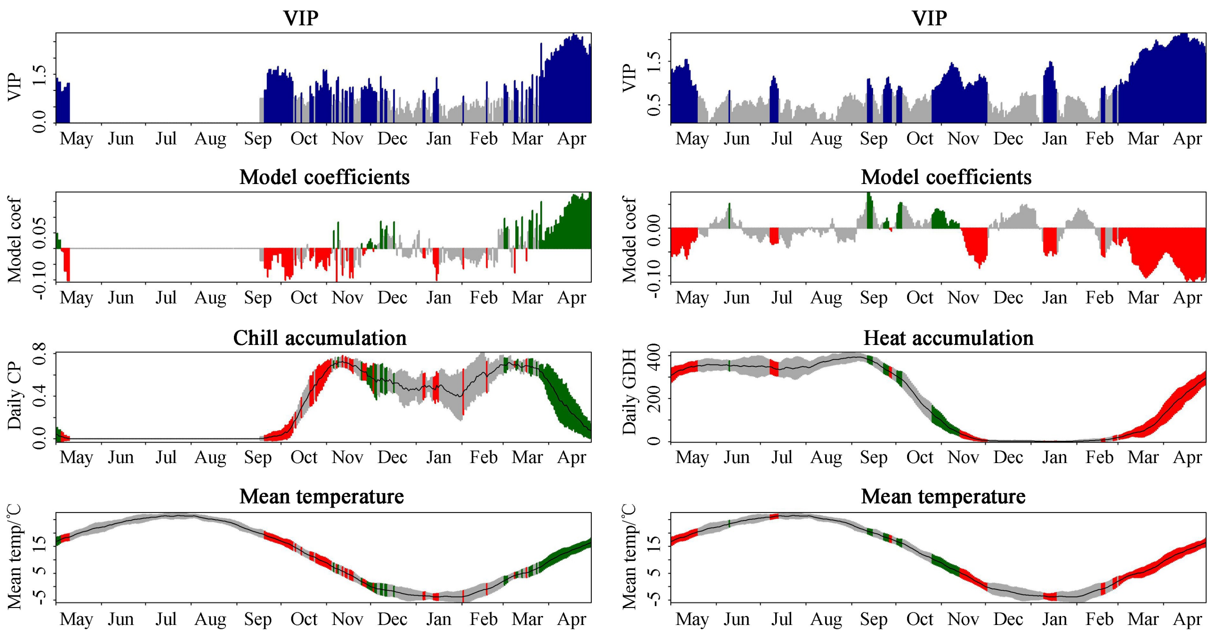

Fig. 2 Results of the PLS regression analysis for leaf unfolding of apricot in Beijing, China during 1963-1988. See captions of Fig. 1 for a full explanation

In Fig. 1, the left panals showed the results of chilling analysis for flowering. Between 17th September and 27th February, model coefficents were mostly negative and VIP values exceeded 0.8 (the threshold for variable importance). However, this period was interrupted by some phases with positive coefficients indicating delaying effects of high chill accumulation on flowering. Since these unexpected periods were short and always unimportant (VIP < 0.8), we interpreted the entire period (17th September to 27th February) as the chilling period of apricot flower buds. The right part of Fig. 1 showed that the forcing period started in early January, but heat accumulation before February was low. Considering the average flowering date (7th April) of apricot, we regarded the period between 15th February and 7th April as the forcing period of apricot flower buds.

Similarly, the chilling and forcing periods of apricot leaf buds were from 17th September to 25th February and from 18th February to 18th April, respectively (Fig. 2). The chilling periods of leaf and flower buds were almost the same, while the forcing period of leaf buds of apricot seemed longer than flower buds, which could partially explain the later occurrence of leaf unfolding.

2.2 Chilling and forcing periods for leafing and flowering of mountain peach

During 1963 – 1988, the average leafing and flowering date of mountain peach in Beijing Summer Palace was the 8th April and 28th March, respectively. For the flowering analysis, daily chilling and heat accumulation rates between the previous April and March were used as independent variables in the PLS regression, while dependent variables were mountain peach flowering dates. For the leafing analysis, daily chilling and heat accumulation rates between the previous May and April were used. Based on the VIP and standardized model coefficients of the PLS regression, chilling and forcing periods for leafing and flowering of mountain peach were identified (Fig. 3-4).

According to the regression results, the chilling and forcing periods of flower buds of mountain peach were from 20th September to 28th February and from 15th February to 28th March, respectively. The chilling and forcing periods of leaf buds were from 17th September to 28th February and from 16th February to 8th April, respectively. The chilling periods for leafing and flowering of mountain peach were the same. However, the forcing period of leaf buds was longer compared with the flower buds.

For apricot and mountain peach in Beijing, the chilling periods and the initial dates of the forcing periods for flowering and leafing were almost identical. Varied end dates of the forcing periods for leafing and flowering were the dominant factors that initiated bloom earlier than leave unfolding.

2.3 Chilling and heat requirements for leafing and flowering of apricot and mountain peach

The chilling and heat requirement values of leaf and flower buds gave clearer explanations for the earlier occurrence of flowering than leaf unfolding (Table 1). The chilling requirements of leaf and flower buds of apricot and mountain peach were almost the same. The greater differences of heat requirements between leaf and flower buds determined the chronological sequence of flowering and leaf unfolding.

Table 1　Estimation of the chilling and heat requirements for leafing and flowering of apricot and mountain peach in Beijing Summer Palace during 1963-1988. CP means Chill Portions, and GDH means Growing Degree Hours

Species (Buds)	Chilling period			Forcing period		
	Start	End	Requirement (CP)	Start	End	Requirement (GDH)
Apricot (Flower)	17th Sep	27th Feb	75.1±5.9	15th Feb	7th Apr	2829.7±876.2
Apricot (Leaf)	17th Sep	25th Feb	73.5±6.3	18th Feb	18th Apr	5209.7±1268.6
Mountain peach (Flower)	20th Sep	28th Feb	75.7±5.9	15th Feb	28th Mar	1457.2±581.2
Mountain peach (Leaf)	17th Sep	28th Feb	75.7±5.9	16th Feb	8th Apr	2992.6±925.0

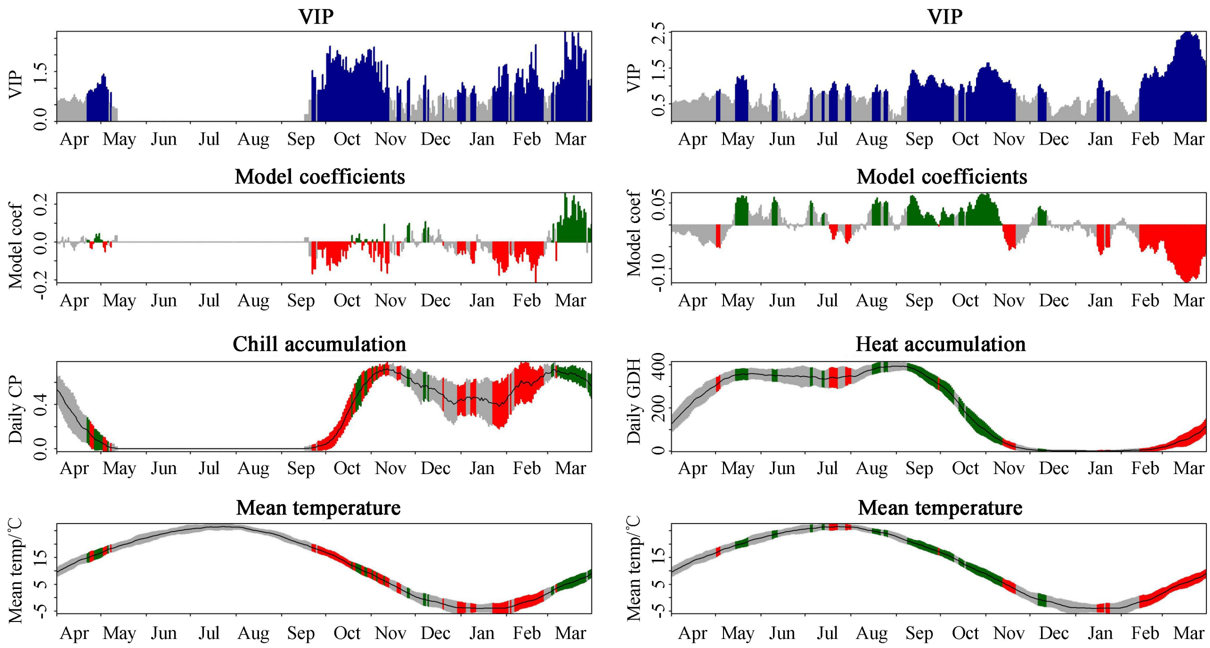

Fig. 3 Results of the PLS regression analysis for flowering of mountain peach in Beijing, China during 1963-1988. See captions of Fig. 1 for a full explanation

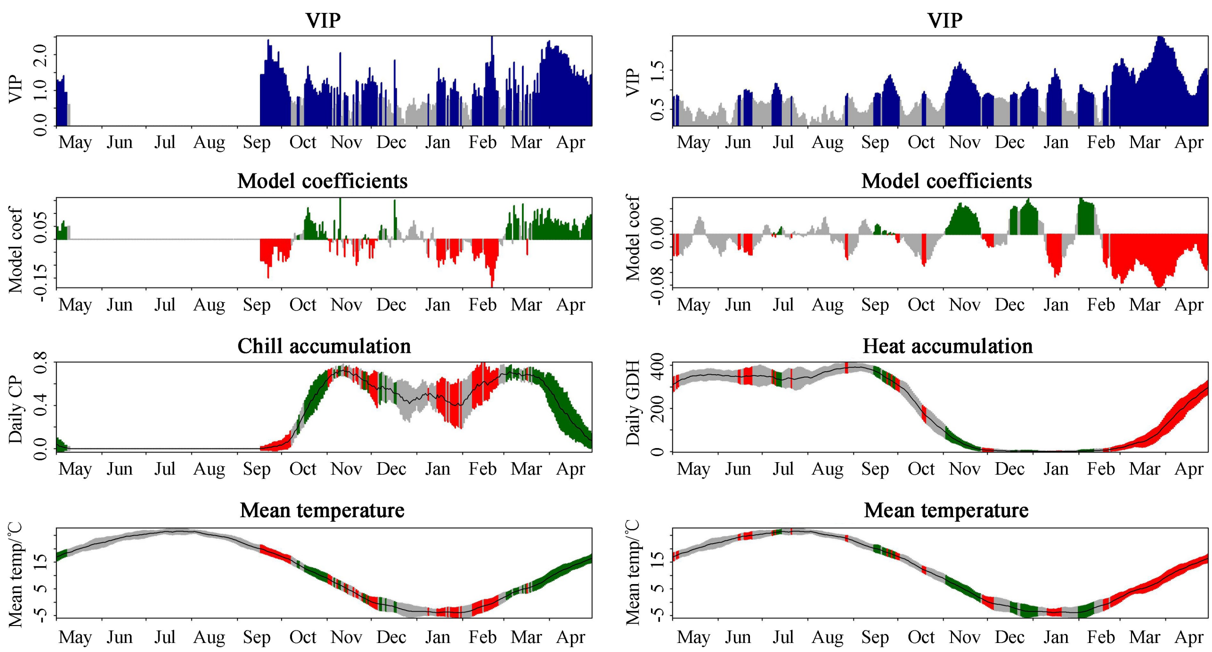

Fig. 4 Results of the PLS regression analysis for leaf unfolding of mountain peach in Beijing, China during 1963-1988. See captions of Fig. 1 for a full explanation

3 Discussion

3.1 Identification of the chilling and heat requirements, and usefulness of our PLS analysis

Different methods have been used to identify the chilling and heat requirements of plants, especially in fruit trees. Valentini *et al.* (2004) collected apricot and peach twigs with dormant buds weekly from November to February and put them into forcing conditions to release dormancy. Sample buds were weighed before and after the forcing period to deter-

mine the time of endodormancy breaking. Chilling and heat requirements of the sample buds were then calculated during the respective periods. In China, this approach was used widely to identify the chilling requirements of different fruits including grape, sweet cherry, peach, plum, apricot, jujube, pomegranate, and fig (Gao *et al*., 2001; Cui *et al*., 2009). Other experimental methods are also in use. To evaluate the chilling requirements of some Asian pear cultivars in Iran, shoot cuttings with flower buds were kept at 4±1 ℃ for different time periods, and subsequently forced in a greenhouse with high temperatures. If 50% of the flower buds sprouted after the forcing, the previous chilling period was assumed to be enough to break the dormancy, and used to calculate chilling requirements (Arzani and Mousavi, 2008). Both methods may not be useful for determining chilling and heat requirements, because they include artificial temperature treatments that do not represent conditions in orchards. Such artificial treatments, especially during the chilling phase, have been shown to lead to misleading results (Luedeling *et al*., 2009b).

Long-term phenological records offer an opportunity for statistically determining the climatic requirements of trees, based on statistical analysis of correlations between the timing of phenological events and daily temperatures. This method has proven useful for estimating chilling and heat requirements of cherry flower buds in Klein-Altendorf, Germany (Luedeling *et al*., 2013).

In our analysis, using daily chilling and heat accumulations instead of pure daily temperatures in the PLS regression allowed more accurate estimation of chilling and heat requirements, because these values should be more representative of the speed of physiological processes in plants than unprocessed temperatures. When long-term phenological observations are available, this approach provides a rapid way to estimate the chilling and heat requirements of plants without extensive experimentation, and could be a more accurate method since it just bases on the natural response of phenology events to chilling and heat accumulations.

3.2 Chilling and heat requirements of leaf and flower buds

Most studies of the climatic requirements of temperate trees have focused on the chilling requirements of flower buds. However, heat requirements of plants are equally important for initiating flowering. The fulfillments of chilling and heat requirements of leaf buds are also vital for leaf unfolding, photosynthesis and vegetation growth of plants. Yet most past studies have focused exclusively on chilling requirements.

Both leaf and flower buds chilling requirements of 65 fruit tree cultivars were estimated experimentally in China, with results indicating that chilling requirements of flower buds were generally slightly higher than leaf buds. The chilling requirements of flower buds of different apricot cultivars varied from 790 to 920 Chill Units (calculated with the Utah Model, another chilling model), while they were 790–910 Chill Units for leaf buds (Gao *et al*., 2001). Similar chilling requirements of both leaf and flower buds were also observed in our study. However, the fruit trees in our analysis displayed huge differences in the heat requirements for flowering and leaf unfolding. Earlier flowering followed by leaf unfolding could be attributed to lower heat requirements compared with leaf buds.

3.3 Importance and urgency of the phenological observations in China

Phenological observations have provided important guidance for agricultural practices, advising farmers on the timing of spring sowing, irrigation, fertilization and crop protection. They are also important for evaluate the risk of frost damage and for forecasting plant development and harvest dates. Recent climate warming has aroused public attention across the world. As the most responsive and easily observable indicator in nature, phenology records have been used to ascertain impacts of climate changes. Variation of plant phenology induced by current

global warming can have significant impacts on plant production (Lobell and Asner, 2003), plant competition (Rathcke and Lacey, 1985) and interactions (Primack *et al.*, 2009), shifts in agricultural zoning (Badeck *et al.*, 2004), pest and disease control (Luedeling *et al.*, 2011) and pollen dispersal forecasts (Traidl-Hoffmann *et al.*, 2003).

Compared with systems in place in Europe, America and Japan, where long-term phenological observation records are being collected from widely distributed observation sites, systematic phenological observations in China started later, and unfortunately stopped in 1988 after observations had been conducted for about 25 years. Abundant biodiversity, a vast land area, and various climatic types in China provide unparalleled opportunities to conduct phenological observations. So it is quite important and urgent to restart the standardized, systematic, comprehensive, and nationwide phenological observations across China.

4 Conclusions

PLS regression between phenological dates and daily chilling/heat accumulation rates proved useful for identifying the chilling and heat requirements of leaf and flower buds when long-term phenological observations are available. For hysteranthous plants, lower heat requirements of flower buds determined the earlier occurrence of flowers compared to leaves, while chilling requirements for leaf unfolding and flowering were similar. Consistent phenological observations should be conducted in China since phenological variation of plants can provide direct evidence of climate change, which is expected to affect plant growth, development and survival in the near future.

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